THE PROLONGED ACTIVITY OF MOMENTARILY STIMULATED NERVES

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According to conventional neuro-physiology a nerve when severed from its center and momentarily stimulated is supposed to respond by momentary activity as is well shown in the single twitch of the attached muscle when a severed motor nerve is subjected to a single electric shock. Such momentary activity does not seem to characterize chromatophoral nerves, for, when cut, they remain active as a result of the severance for many hours or even days. This condition is illustrated in the responses of the melanophore nerves in the caudal fins of many bony-fishes.

If one or more bony rays in the tail-fin of a catfish (Ameiurus) or of a killifish (Fundulus) are completely severed near the root of the tail together with their accompanying nerves, the melanophores in the radial band thus denervated pass quickly into a state of dispersed pigment whereby the band becomes noticeably dark (Fig. 1). This dark band reaches a maximum depth of tint in a few hours and then gradually fades till it attains the general tint of the fish in from a day or so to a week. The continuation of this state over so long a period is believed to be due to the continued activity of the severed nerve-fibres.

Instead of the interpretation just given it might be assumed that the nerves whose severance brings about a dispersion of the melanophore pigment exert an inhibitory action on this response and that when they are cut the melanophores react as to a release from this inhibition. But this view can be shown not to be sound by what is to be observed when a cold-block is applied to the nerve. Drugs cannot well be employed for this purpose for the following reasons. The radial nerves in the tail-fin of the killifish are at best not over a centimeter and a half long and any drug applied to the middle of such a nerve quickly spreads along its length and may thus directly affect the associated melanophores. Cold, however, can be used as a block with full satisfaction.

If the tail of a living killifish is spread out on a white board and a bent capillary glass tube is applied for about two millimeters of length transversely to its rays and on the middle of their length, a cold fluid (50 per cent alcohol) can be run through the tube so as to chill the nerve to a few degrees below freezing. In the actual tests the cold alcohol mixture left the reservoir at about $-13°$C. and emerged after its passage over the nerve at from $-1°$ to $-2°$C.

When radial nerves are thus chilled impulses causing the dispersion of

melanophore pigment are blocked. This can be shown by cutting such nerves proximal to the chilled area. On carrying out such an operation the denervated band quickly darkens from the cut to the chilled area which, however, the dark band neither enters nor passes. If the nerves distal to the chilled area are cut the distal region darkens from the new cut to the edge of the fin (Fig. 2). These observations show that the nerves both proximal and distal to the chilled area are normally active and, what is equally important, that the chilled area is a complete block for impulses concerned with melanophore changes. If on thus blocking these impulses the distal melanophores show no change, as is the case, we are warranted in believing that the impulses that naturally pass over these fibres are not inhibitory impulses but those concerned with positive excitation.

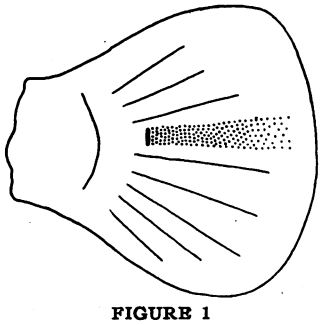

FIGURE 1

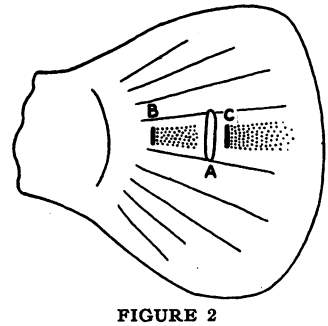

FIGURE 2

Figure 1.—Caudal fin of a killifish (Fundulus) showing a band of dark melanophores produced by the severance of radial nerves near the root of the tail.

Figure 2.—Caudal fin of a killifish across a part of which a capillary tube (*A*) carrying a freezing mixture has been placed. The cut (*B*) proximal to the tube has been followed by the formation of a dark band which reaches from the cut to the chilled area but does not enter it; the cut (*C*) distal to the tube has been followed by the formation of a band which reaches to the edge of the fin.

It might be supposed, however, that the quick darkening in the formation of the bands and their slow fading is a reflection of gradual degeneration in the nerve-fibres, a phenomenon that is well known to occur in these very nerves (Parker and Porter, 1933). But if a band is allowed to fade, which may occur, as already stated, in a day or more, and a new and shorter cut is made within the area of the band and distal to the original one, a smaller but well defined band within the limits of the first will quickly develop (Fig. 3). This shows at once that the nerves are still active and have not yet suffered even the early stages of degeneration. The appearance and disappearance of the band, therefore, is not to be attributed to degeneration.

It might be assumed since the exciting cut severs small bony rays and

since the tail is in more or less continual movement that these cut rays rub the severed ends of the nerves and thus continually excite them to action till this condition is overcome by eventual healing. If, however, in place of a simple transverse cut in the tail, a square hole is made in it so that the ends of the cut rays cannot rub against the nerves, this possible source of stimulation can thus be removed. Under such circumstances the dark band forms as quickly and as fully as it does from the simple transverse cut (Fig. 4). The rubbing of the cut fin-rays on the severed ends of the nerves then appears to play no essential part in the activation of the melanophore nerves.

In consequence of these several observations I am led to conclude that the nerve-fibres concerned with the dispersion of melanophore pigment even when separated by severance from their nerve centers, continue to

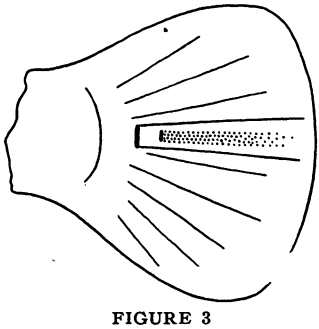

FIGURE 3

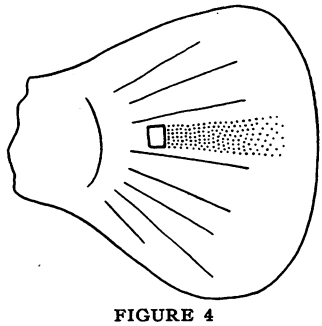

FIGURE 4

Figure 3.—A faded band in the tail of a killifish within which a new short cut has been made. This cut has induced the formation of a new small band within the larger one showing that the severed nerve-fibers of the original band are still active.

Figure 4.—A band in the tail of a killifish produced by cutting a hole instead of making merely a slit.

act in a positive way and over a long period of time on their appropriate effectors. This conclusion, moreover, is supported by experiments with adrenalin. If a small dose of adrenalin is injected into a killifish with a well-marked caudal band, the fish quickly becomes very light in tint and the dark caudal band fades completely. After 4 to 5 hours the effect of the adrenalin wears off and the fish gradually assumes its slightly darker tint. At the same time and without any further stimulation the dark band returns in its entirety. The original dose of adrenalin carried in the blood of the fish must have acted directly on the melanophores and in its characteristic way by inducing a concentration of the pigment. As this hormone disappeared, the dispersing nerves, whose action had been overridden by the adrenalin, must have begun to reassert themselves and the dark band consequently reappeared. This at least seems to be the most

plausible explanation of the conditions herein described and rests on the idea of continuous nervous activity even to the extent of the recovery of the band.

How the band recovers is an interesting question. The positive action of the nerve-fibres whereby the band is excited is believed to be due to the discharge from the activating nerve terminals of a neurohumor which when it reaches the melanophores induces them to disperse their pigment. Is the band after excitation maintained by a relatively large amount of locally held neurohumor or do the nerve-fibres after severance continue to produce this substance but in gradually diminishing amounts till they cease completely? This question may be tested by applying a cold-block, as already described, to the middle of a fully developed dark band. If the band is maintained by an initial and excessive discharge of neurohumor stored for the time being in the tissues, the distal half of the band after the application of the block ought to show no change. If, however, the band is maintained by a more or less continuous flow of impulses from the cut to the distally located melanophores, on the interruption of this flow by the block the distal part of the band ought to fade. As a matter of fact when this test is applied the distal half of the band does fade and fade unequivocally (Fig. 5). This condition is best seen in bands on the tail of the killifish which have about reached their maximum tint rather than in freshly excited bands. From the outcome of these tests the conclusion is again warranted that severed melanophore nerves are for a long time thereafter continuously active.

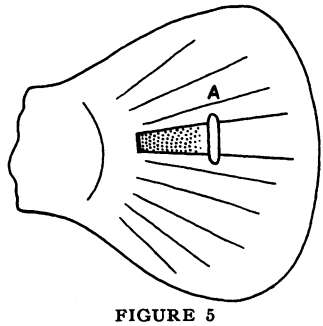

FIGURE 5

A fully formed band in the tail of a killifish to which a cold block (*A*) had been applied with the result that the distal half of the band faded in about a quarter to half an hour after the application of the block.

The nerve-fibres that are concerned with the melanophore responses in fishes have long been known to be of autonomic origin and those having to do with the dispersion of pigment are presumably parasympathetic in their source. Such fibres are non-medullated and to this condition might be ascribed their apparently exceptional peculiarities, for the general belief of neuro-physiologists in the inactivity of nerves separated from their centers is based upon the study of medullated elements. It must be admitted, however, that the nerve-fibres concerned with pain, fibres that are known to be medullated, may show more or less continuous functional activity not unlike that just described for the melanophore nerves. Moreover, by means of oscillograph methods Adrian (1930)

has identified post-operative discharges from mammalian medullated nerves and more recently Hoagland (1933) has recorded similar conditions in the lateral-line nerves of fishes. I am, therefore, led to conclude that probably many nerves, medullated as well as non-medullated, may remain more or less continuously active for long periods, days in fact, after their severance from their centers. This conclusion is put forward notwithstanding the fact that many neuro-physiologists hold a contrary opinion.

Adrian, E. D., "The Effects of Injury on Mammalian Nerve Fibres," *Proc. Roy. Soc. London*, **B106**, 596–618 (1930).

Hoagland, H., "Electrical Responses from the Lateral-Line Nerves of Fishes. IV. The Repetitive Discharge," *Jour. Gen. Physiol.*, **17**, 195–209 (1933).

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*THE CENTRAL NERVOUS MECHANISM FOR EMOTIONAL RESPONSES: II. A TECHNIQUE FOR DESTROYING THE DEEPER NUCLEAR REGIONS WITHIN THE CEREBRUM WITH A MINIMAL DESTRUCTION OF THE INTERVENING CORTEX**

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Previous studies on the neural bases of emotional responses have indicated that certain nuclear regions in the thalamus are functionally significant in the rage response whenever these regions are released from the control of the cerebral hemispheres (Bard,[1] de Barenne[3] and Weed[7]). In these investigations acute decorticate or decerebrate preparations were used. The areas isolated for study were large and rather poorly defined. The intense responses involved in self protection, and usually termed rage responses, dominated the behavior of the animals and prevented the appearance of other types of emotional reactions.

In reviewing these studies a number of questions have arisen concerning the neural bases of emotional responses. First, would the functions of these deeper nuclei be different when the restraining influence of the cortical centers are removed than when these centers are intact? In order to test this a technique must be used which will allow for the destruction of the deeper nuclei with a minimal destruction of the overlying cortex. Second, are the neural bases for emotional responses localized within a definite, small nuclear region within the mesencephalon or diencephalon, or a number of these regions? To answer this question a method must be devised